

*UNDERWATER AUDIOGRAM OF THE  
CALIFORNIA SEA LION BY THE CONDITIONED  
VOCALIZATION TECHNIQUE<sup>1</sup>*

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Conditioning techniques were developed demonstrating that pure tone frequencies under water can exert nearly perfect control over the underwater click vocalizations of the California sea lion (*Zalophus californianus*). Conditioned vocalizations proved to be a reliable way of obtaining underwater sound detection thresholds in *Zalophus* at 13 different frequencies, covering a frequency range of 250 to 64,000 Hz. The audiogram generated by these threshold measurements suggests that under water, the range of maximal sensitivity for *Zalophus* lies between one and 28 kHz with best sensitivity at 16 kHz. Between 28 and 36 kHz there is a loss in sensitivity of 60 dB/octave. However, with relatively intense acoustic signals ( $> 38$  dB re  $1 \mu\text{b}$  underwater), *Zalophus* will respond to frequencies at least as high as 192 kHz. These results are compared with the underwater hearing of other marine mammals.

Underwater sound-production and reception capacities of marine mammals have only recently been appreciated. That such capacities exist and frequently appear to be uniquely suited to the ecological demands made on various marine mammal species has now been documented. However, research emphasis, in both the field and the laboratory (Evans, 1967; Norris, 1969); has largely concentrated on understanding the nature of autocommunicative (echolocation) and social communicative acoustic signals emitted by odontocete whales and by seals and sea lions (Evans and Bastian, 1969; Norris, 1969; Schusterman, 1968). More than half of the 117 marine mammal species listed by Rice and Scheffer (1968) are known to emit underwater sounds (Poulter, 1968) and the emitted sound repertoires of about 20 of these species have undergone or are currently undergoing detailed acoustical analyses.

In contrast, there is very little information in the open literature on the auditory sensitivity of marine mammals. Only one pinniped species of the family *Phocidae*, the harbor seal (*Phoca vitulina*), and only one odontocete cetacean, the Atlantic bottlenosed porpoise (*Tur-*

*siops truncatus*), have been studied in enough detail to know their sound-detection thresholds over a wide range of relatively pure tone frequencies, and in both instances a single animal was studied (Møhl, 1968a; Johnson, 1966). [Terhune and Ronald (in press) studied the underwater hearing of the harp seal (*Pagophilus groenlandicus*) at the same time that the present investigations were conducted.] In order to understand the significance of a given species' underwater phonations, it is of utmost importance to obtain information on its hearing capacities. For example, if a given marine mammal species is supposed to locate its food source by means of an active sonar system, then is its hearing suitable for this task? Furthermore, information relating the underwater hearing capabilities of a wide taxonomic range of marine mammals to the anatomical structures of their auditory systems should provide important clues regarding the structural modifications of the acoustical apparatus that are necessary for sensitive and acute underwater hearing.

Johnson (1966) obtained pure tone thresholds from a porpoise over the frequency range of 75 Hz to 150 kHz and Møhl (1968a) determined both underwater and aerial pure tone thresholds in a harbor seal. The frequencies used under water by Møhl ranged from 1 to 180 kHz. Both investigators used operant conditioning techniques in which their animals reported the presence of a tone by nose-press-

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ing a lever and the absence of a tone either by not responding (porpoise) or by pressing a second lever (seal). Both researchers controlled for "false positives" by using catch trials and either a timeout procedure (porpoise) or an airblast punishment (seal) as a consequence for incorrect responses. The difficulties involved in making measurements of the sound field with some degree of accuracy as well as ensuring attention of the animals to the conditioned stimuli were solved in both cases by training the animal to orient its head in approximately a fixed position relative to the sound source before the onset of the conditioned stimulus. Møhl trained his seal to turn the conditioned stimulus on; by so doing, the seal's head was always in a fixed position to receive the sound signal. Johnson trained his porpoise always to place its head in a stall-like enclosure before the onset of a sound signal. The results of these experiments clearly showed that both the seal and the porpoise are at least as sensitive to sound under water as man is in air.

The present research was concerned with the general hearing capacities of the otariid pinnipeds. More specifically, this paper discusses the underwater sound-detection thresholds in the California sea lion (*Zalophus californianus*). An audiogram—i.e., sound detection thresholds over a wide range of relatively pure tone frequencies—was generated by using conditioned vocalization as an objective index as to whether a sea lion heard a tone under water.

## METHOD

### *Subject*

The experimental animal was a 5 to 6-yr-old male *Zalophus* (Sam) weighing approximately 160 kg. The animal had been in captivity for over 4 yr and had been used before in a variety of visual discrimination tasks (Schusterman, 1968). Just before the beginning of the present experiment, Sam had had intensive training in emitting underwater click bursts on viewing a striped target and in remaining silent when viewing a gray target (Schusterman and Balliet, 1970).

### *Sound Equipment and Measurement*

Underwater thresholds were obtained in a 15 by 30 by 6 ft (4.6 by 9.1 by 1.8 m) oval-

shaped redwood tank. Two projectors were used. A moving coil transducer (J-9) and a lead zirconate titanate transducer (F-41) were supplied and calibrated by the Underwater Sound Reference Division of the Naval Research Laboratory at Orlando, Florida and were mounted side by side, 3.3 ft (1 m) from the bottom at one end of the tank facing the longest dimension. A headrest position in the tank was determined by using a continuous 1000-Hz sine wave to "search" the area where the radii of the end and side intersect with a H-23 hydrophone to find the place where the amplitude of the sine wave was maximum. The headrest was positioned at this point in such a way as to ensure that the sea lion's skull would be located where the maximum sound level occurred. The sea lion's head was positioned approximately 6.6 ft (2 m) from the sides of the tank and 3.3 ft (1 m) from the projectors (see Figure 1).

With the H-23 hydrophone positioned where the animal's head would normally be during testing, 5-msec tone bursts were produced by the J-9 projector at 1000 Hz and successive octave intervals up to 8000 Hz. The electric signal was gated with instantaneous rise-decay time and monitored on one channel of a dual-beam oscilloscope. The output of the H-23 hydrophone was monitored by the second channel, and the amplitudes of the return echoes were noted. Above 4000 Hz, echo amplitudes were unmeasurable; i.e., they were below either the ambient noise level of the tank or the electrical noise of the system. Signal duration was then increased to 500 msec, and the rise-decay was adjusted so that, for the 1000-Hz signal, no increment was added to the waveform envelope by any return echoes. The rise-decay time necessary for this condition was 100 msec.

The H-23 hydrophone was used to determine signal level at each frequency. Acoustic signals were gated using a Grason-Stadler 829E electronic switch. Gate duration was controlled by an Iconix preset counter and logic system. A General Radio 1312 decade oscillator was used to generate the signals. Two Daven 2-dB step attenuators in series fed signals into a McIntosh 75-w audio amplifier and controlled the signal level. The output of the McIntosh amplifier was led directly either to the J-9 or F-41 projector. Voltage across the transducer was calibrated before

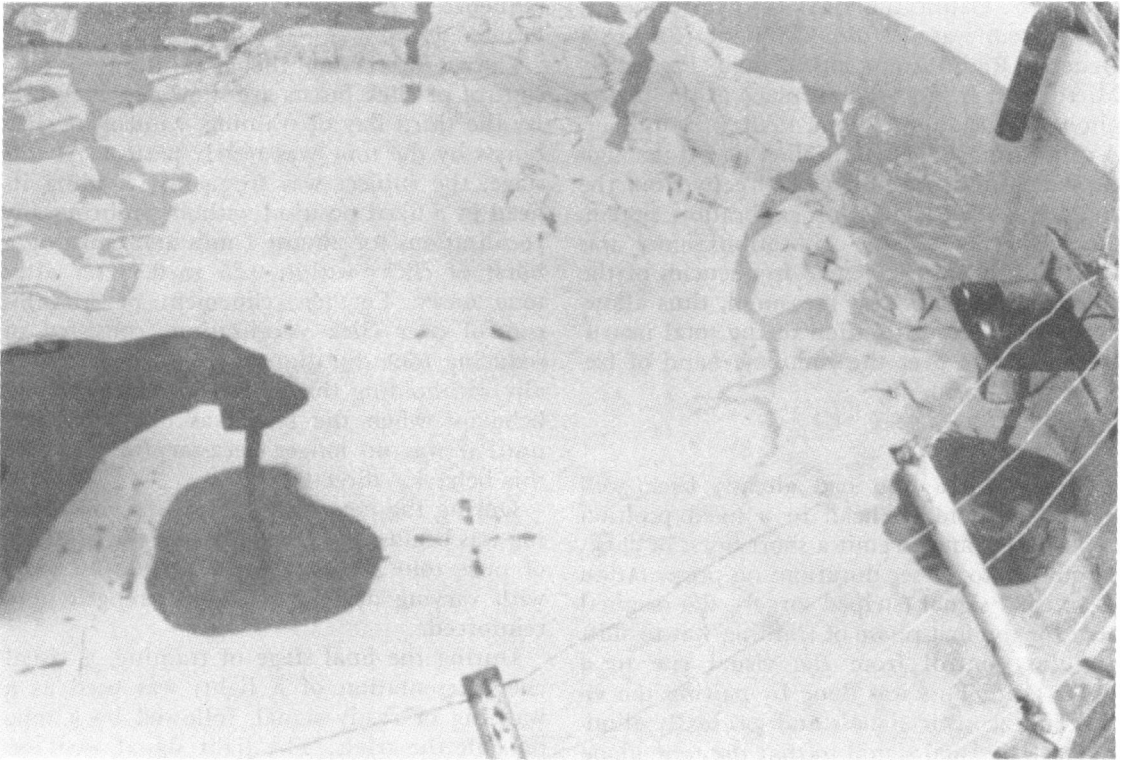


Fig. 1. Sea lion waiting for warning signal (projectors are on the right).

each test session and was continuously monitored using a Hewlett-Packard 132A dual-beam oscilloscope.

Ambient acoustic noise under water was measured in one-third octave bands across the frequency range of 100 to 20,000 Hz. Table 1 presents these measurements for those frequencies used in producing the underwater audiogram for *Zalophus*.

Table 1  
Ambient Noise Levels  
(dB re 1  $\mu$ b)

Frequency (kHz)	One-Third Octave Band	Spectrum Levels
0.25	-31	-49
0.50	-26	-47
1	-30	-53
2	-35	-62
4	-35	-64
8	-35	-67
16	-34	-70
20	-35	-72

Accuracy of the noise measurements was ensured by using a U.S. Navy standard hydro-

phone model H-56, recently supplied and calibrated by the Underwater Sound Reference Division of the Naval Research Laboratory at Orlando, Florida. To guarantee accuracy further, the complete instrumentation and analysis equipment was battery powered, thus isolating it from the effects of powerline electrical noise and the associated ground loops, which could have a significantly deteriorating effect on these low-level measurements.

The output signal from the H-56 hydrophone (Serial No. 3, sensitivity -75 dB reference 1 v per microbar) was fed to a Princeton Applied Research (PAR) low-noise amplifier, model CR4-A, for preamplification and broad bandpass filtering. The resultant signal was further amplified using a Burr-Brown variable gain amplifier model 110, was monitored by an oscilloscope, and then was presented for one-third-octave band analysis. This analysis was performed using a General Radio Company Sound and Vibration Analyzer Type 1554A, which incorporates accurate one-third-octave band tunable filter sets. Using this instrument, data were gathered, checked, and

analyzed. Calibration of the instrumentation system was performed by substituting a General Radio Company Audio Frequency Microvolter Type 546C in place of the hydrophone at the input of the PAR preamplifier. A calibration signal could then be fed through all the equipment and read directly from the analyzer. Also, using this calibration system, the frequency of the calibration signal was varied to match the center frequencies of the one-third-octave bands measured, thus allowing a complete calibration of the total instrument package over the complete band of frequencies measured.

### *Training Procedure*

Since the sea lion had already been well trained to hold its head in a fixed position under water and to emit a short burst of clicks (about 0.5- to 2.0-sec duration) on presentation of a visual signal (striped target), the original plan for the first phase of training was to shift stimulus control from the visual cue to a 6-kHz tone. This was done by pairing the visual and acoustic signals and gradually eliminating the visual signal so that the tone alone eventually controlled all vocal emissions. However, this attempt was unsuccessful, probably because the animal had already been so well trained with the visual signal. Instead, an attempt was made to increase the operant level of click bursts without any stimulus control while the subject maintained its head in a fixed position on the head holder. This was accomplished by withholding the cues (striped targets) associated with the primary reinforcer (fish) while the animal was in the situation where it anticipated such presentations. Once the sea lion began emitting bursts of clicks, "tone-no tone" discrimination training was initiated by presenting a 6-kHz tone for 10 sec or less, interspersed by silent periods. If it emitted a click burst while the tone was still on, a piece of fish was presented, and the tone was turned off as soon as the fish was swallowed. If it remained silent for 10 sec, no tone was presented, and again a piece of fish was presented. A burst of clicks during a silent period postponed reinforcement and reset the clock for another 10 sec. On the first two days of discrimination training, the ratio of no-tone periods to tone periods was set at 3:2. Thereafter, there was an equal number of periods in which a tone was or was not presented. The

sequence of periods was determined by a Gellerman series.

Curves describing the acquisition of tone control of click bursts are shown in Figure 2. By the third day of training, control of click bursts by the tone was nearly perfect. At this stage, the subject was frequently holding its head in a fixed position without emitting any vocalizations for almost 1 min and emitting a burst of clicks within 0.25 to 0.50 sec after tone onset. Further refinement of stimulus control over click vocalizations consisted of reducing tone duration to 0.5 sec and gradually withholding the fish for silent or waiting behavior when the tone was not presented, until it was no longer necessary to reinforce this behavior directly.

During the next stage, generalization training was begun, and click bursts in the presence of pure tone frequencies (1 kHz to 16 kHz) with varying degrees of signal strength were reinforced.

During the final stage of training, a visual cue (presentation of a light) was used as a warning or ready signal, followed by a tone on half the trials. The light signal went on 2 sec before the tone and went off at the same time the tone went off, *i.e.*, after 2.5 sec. After approximately 50 pairings of light and tone, Sam began anticipating the tone by vocalizing to the light. However, vocalizations to the light were readily extinguished by not reinforcing vocalizations that occurred before tone onset.

### *Threshold Testing Procedure*

A single trial consisted of either the presentation of a light [a 150-w floodlight mounted in a window of the tank located next to the projectors (see Figure 1)] that was turned on for 2.5 sec, or the presentation of a light with a tone turned on during the last 0.5 sec of the 2.5-sec light duration. During any test run, half the trials consisted of light-only trials (blank or catch trials) randomly interspersed with light-tone trials (signal trials). A trial was initiated by the experimenter only after he was certain that the animal was in position and, due to the relatively exposed location of the tank, that no noticeable increase in environmental noise was occurring. A "correct" response was defined as either emitting a burst of clicks within 1.5 sec of tone onset or remaining silent for 3.5 sec

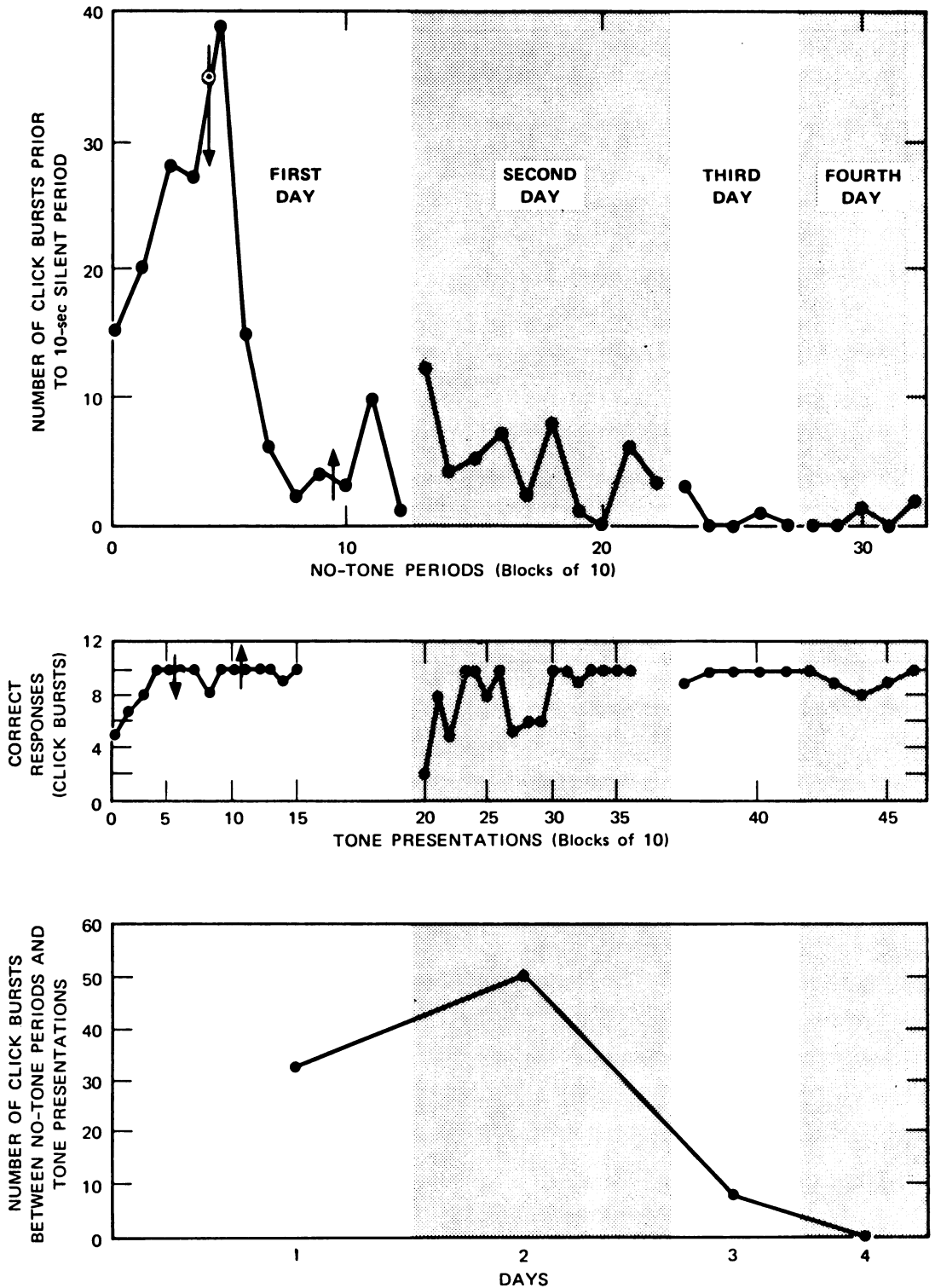


Fig. 2. Acquisition of tone control of click bursts from California sea lion (Sam). Arrows in the upper two graphs indicate tone and no-tone periods that were not determined by a Gellerman series but consisted of long runs (10 to 20) of tones followed by long runs of no tones.

after light presentation. There was no difficulty in defining a correct response since duration of click bursts was between 0.5 and 2.0 sec. The experimenter worked from behind an opaque screen presenting light and light-tone trials by means of a remote switch, recording responses of the sea lion, changing attenuator settings, observing the animal, monitoring acoustic signals, and reinforcing all correct responses by throwing a small piece of herring to the sea lion. Sound production of the animal was continuously monitored by means of a hydrophone. To ensure that the sea lion was not responding to any cues from the sound-generating and monitoring equipment, several threshold tests were conducted, including not only blank trials in which there was no presentation of a tone (signal generator inoperative) but also blank trials in which the signal was attenuated 24 to 76 dB below the sea lion's estimated threshold.

A modified method of limits similar to the "staircase method" was used to obtain all sound-detection thresholds (defined as the interpolated dB values at which the sea lion responded correctly 75% of the time; see Figure 3) at each of the frequencies tested, ranging from 250 to 64,000 Hz. A range of acoustic signal strengths was explored in single-trial steps of 10 dB at the start of each daily threshold test session with a single frequency that had not previously been presented. Thereafter, during each test, the intensity of the tone was decreased in steps of 4 dB if the sea lion succeeded in making seven or more correct responses in 10 successive trials (five signals and five blanks). If the sea lion committed four or more errors, the intensity of the tone was increased by 12 dB. This latter procedure ensured a stable conditioned vocalization. Thus, the strength of the acoustic signal was changed every 10 trials. A session was terminated only after the animal had made seven of 10 correct responses at a given signal strength. Usually the animal received 150 trials, 75 blank trials and 75 signal trials. Thresholds were obtained this way at least twice for each frequency tested, and, in most cases, three or four threshold determinations were made (see Table 2). The first frequency chosen was 1000 Hz with each octave or half-octave frequency being tested in succession until 32, 48, and 64 kHz were tested. Initially, the sea lion responded poorly or not at all to

these frequencies, and the conditioned vocalization had to be reinstated with tones of lower frequencies. One to three months later, after intensive training with frequencies at and above 32 kHz, relatively smooth psychophysical functions were obtained with intense acoustic signals, and thresholds at the higher frequencies were obtained.

## RESULTS

The threshold estimates at each of the frequencies tested, along with the dates of testing are shown in Table 2. The J-9 projector was used to obtain all thresholds for frequencies at and below 32 kHz, while the F-41 projector was used to obtain all thresholds for frequencies at and above 32 kHz. Figure 3 shows the psychophysical functions at each of the frequencies tested. The curves are based on the combined data for each frequency (except 32 kHz) and show the method for estimating the mean thresholds that were used to construct the audiogram presented in Figure 4. Thresholds may be found in the graphs shown in Figure 3 by noting the intensity associated with 75% correct responses. The curve through all data points of the audiogram, except at 32 kHz, was derived in this manner. The individual data points shown in Figure 4 were generated from psychophysical curves plotting daily performance as a function of sound intensity.

Table 2 shows that, at several frequencies, threshold measurements were repeated at widely disparate times, and, except for 32 kHz, the variability at most frequencies was either moderate or low (*e.g.*, 4, 16, and 24 kHz). The greatest difference was 11 dB at 8 kHz. The first four threshold estimates at 32 kHz with the J-9 projector were consistent but relatively high. Measurements made six and then 14 weeks later with the same projector yielded threshold values averaging 20 dB less than the initial estimates. Measurements made with the F-41, a more efficient projector at 32 kHz than the J-9, yielded thresholds that fell between the earlier and later thresholds obtained with the J-9 projector.

Since the one-third octave band ambient noise levels at each of the frequencies tested were 10 to 20 or more dB below the obtained thresholds, it is unlikely that the shape of the audiogram in Figure 4 was very much influ-

Table 2  
Sound Detection Thresholds in a California Sea Lion (SAM)

Frequency	Date Tested	Threshold (dB re 1 $\mu$ b)	Frequency	Date Tested	Threshold (dB re 1 $\mu$ b)
250 Hz	10/12/70	+ 16	28 kHz	8/28/70	- 14
250	10/13/70	+ 9	28	8/31/70	- 17
250	10/14/70	+ 16	32	7/14/70	+ 9
500	10/6/70	- 6	32	7/15/70	+ 9
500	10/7/70	- 6	32	7/22/70	+ 13
1 kHz	6/8/70	- 13	32	7/23/70	+ 13
1	6/12/70	- 20	32	9/1/70	- 8
1	6/18/70	- 13	32	9/2/70	- 5
2	6/26/70	- 23	32	10/20/70	- 4
2	7/1/70	- 13	32	10/21/70	- 11
2	9/11/70	- 20	32	10/22/70	- 9
4	7/2/70	- 14	32	10/5/70	+ 3 (F-41)
4	7/3/70	- 13	32	11/10/70	+ 4 (F-41)
4	9/10/70	- 14	32	11/11/70	+ 4 (F-41)
8	7/7/70	- 21	36	10/29/70	+ 27
8	9/8/70	- 17	36	10/30/70	+ 29
8	9/9/70	- 13	36	11/2/70	+ 22
8	12/7/70	- 24	36	11/3/70	+ 29
16	7/8/70	- 20	48	9/3/70	+ 36
16	7/9/70	- 24	48	9/4/70	+ 36
16	8/18/70	- 20	48	10/26/70	+ 40
24	7/10/70	- 20	48	11/13/70	+ 36
24	7/13/70	- 19	48	11/20/70	+ 36
24	8/24/70	- 13	64	11/16/70	+ 46
24	8/25/70	- 13	64	11/17/70	+ 45
			64	11/18/70	+ 44

enced by masking effects, especially at the higher frequencies. The most salient characteristics of the audiogram are: (a) overall maximal sensitivity or lowest thresholds occur between 1 and 28 kHz, thus covering nearly a five-octave range; (b) peak sensitivity or lowest threshold was at 16 kHz; (c) the thresholds rise somewhat sharply below 500 Hz and very sharply above 28 kHz at about 60 dB/octave with the "conventional" or effective upper limit of hearing lying between 36 and 48 kHz; and (d) instead of the curve continuing to rise above 48 kHz, it begins to flatten out. Thus, although there is a loss of about 42 dB when going from 28 to 36 kHz, there is only a 7 dB loss when going from 48 to 64 kHz.

## DISCUSSION

### *Conditioned Vocalization*

Conditioned vocalization (click bursts) proved to be a reliable procedure for obtaining underwater sound detection thresholds in *Zalophus*, as witnessed by the relatively consistent daily thresholds obtained by repeated measurements over periods up to three months.

The technique usually produced smooth psychophysical functions relating correct responses to tone intensity, thus allowing a rather precise definition of thresholds for generating an audiogram. On signal trials, most click bursts, regardless of the frequency and intensity of the tone, occurred while the warning signal light was still on. Occasionally, when the acoustic signal was close to threshold, vocalizations occurred within 1 sec of light and tone termination. Rarely did the sea lion vocalize when the light first came on or between trials (onset of the light).

Despite the very different indicator responses used by the harbor seal (Møhl, 1968a) and the California sea lion, their response criterion for sound detection was apparently quite high. Response criterion is reflected in the rate of false alarms. At 8 and 16 kHz, the overall rate of false alarms was 0.02 and 0.06 for the harbor seal and 0.12 and 0.07 for the California sea lion.

### *Overall Sensitivity*

Since the characteristic acoustic impedance of water is nearly 4000 times the characteristic impedance of air, a pressure wave in air

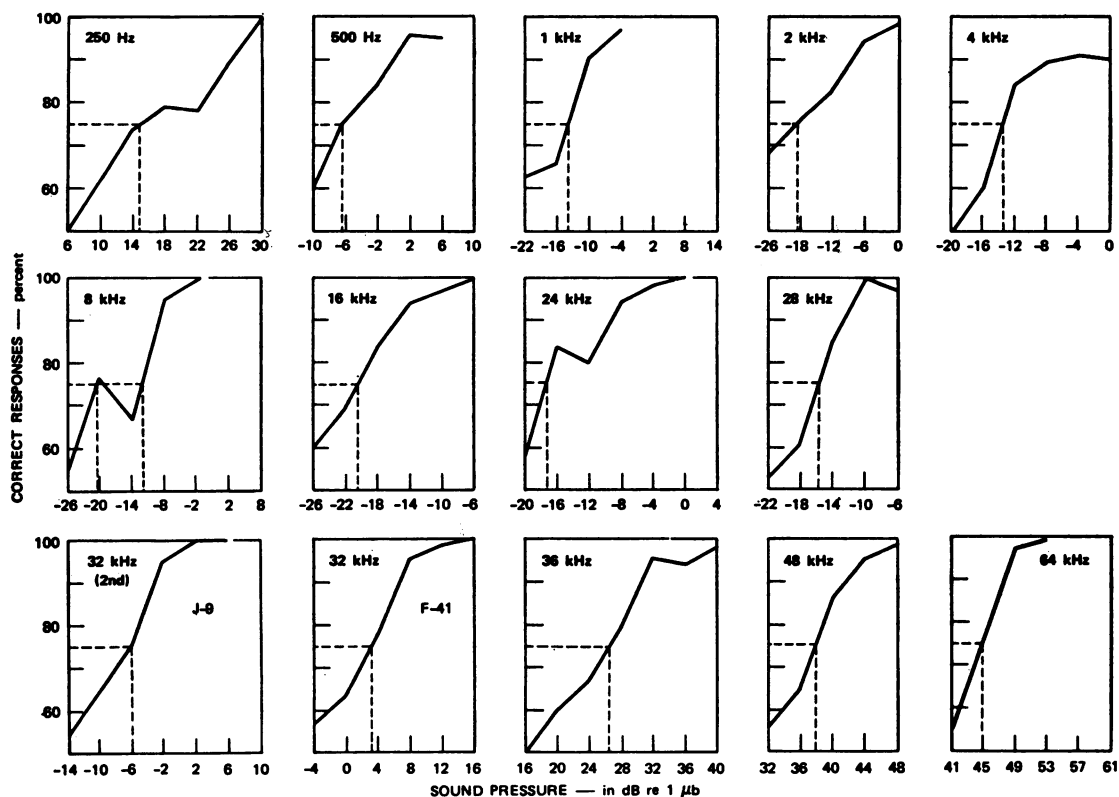


Fig. 3. Percentage of correct responses as a psychophysical function of intensity at each of the frequencies tested. Dashed lines show threshold calculation.

of 0 dB re  $2 \times 10^{-4}$  dynes/cm<sup>2</sup> (−74 dB re 1  $\mu$ b) has the same acoustic intensity as a pressure wave of −38.5 dB re 1  $\mu$ b in water. Considering the higher impedance of water over that of air, the peak sensitivity of the harbor seal under water (at 32 kHz), as reported by Møhl (1968a) is only 1 dB inferior to the ASA standard for acoustic power based on the human threshold in air. On the other hand, the peak sensitivity of the California sea lion under water (at 16 kHz), as obtained in this study, is about 15 dB inferior to that of the harbor seal (see Figure 5). Does this unfavorable comparison of sea lion hearing relative to the seal's hearing under water mean that the ear of the sea lion is less well adapted for hearing under water than that of the seal? At this time, it is premature to draw any such conclusion. At their best frequencies, the 15 dB difference between Møhl's harbor seal and this study's California sea lion can be partially attributed to a variety of methodological differences between the two experiments. These include fluctuation in noise levels, tone dura-

tion, psychophysical procedures, and indicator responses. Also, the 15-dB difference between the peak sensitivity of seal and sea lion could be attributed to individual variation within the species rather than to variation between the two species. Additional data on more individuals and other species of pinniped are required before any conclusions regarding species differences can be made.

The underwater audiograms of the sea lion and seal are similar to each other and to a wide range of other mammals (for a review, see Masterton, Heffner, and Ravizza, 1969) in that they show relatively good sensitivity compared with birds (Schwartzkopff, 1955) and reptiles (McGill, 1960) over a broad range of frequency intervals covering four to five octaves. This is in contrast to recent findings showing that the rat (Gourevitch and Hack, 1966) only has a one-octave range of maximal sensitivity. It has been suggested by Gourevitch and Hack (1966) that a wide range of high sensitivity, as shown by both the sea lion and seal, may be traced to the innervation



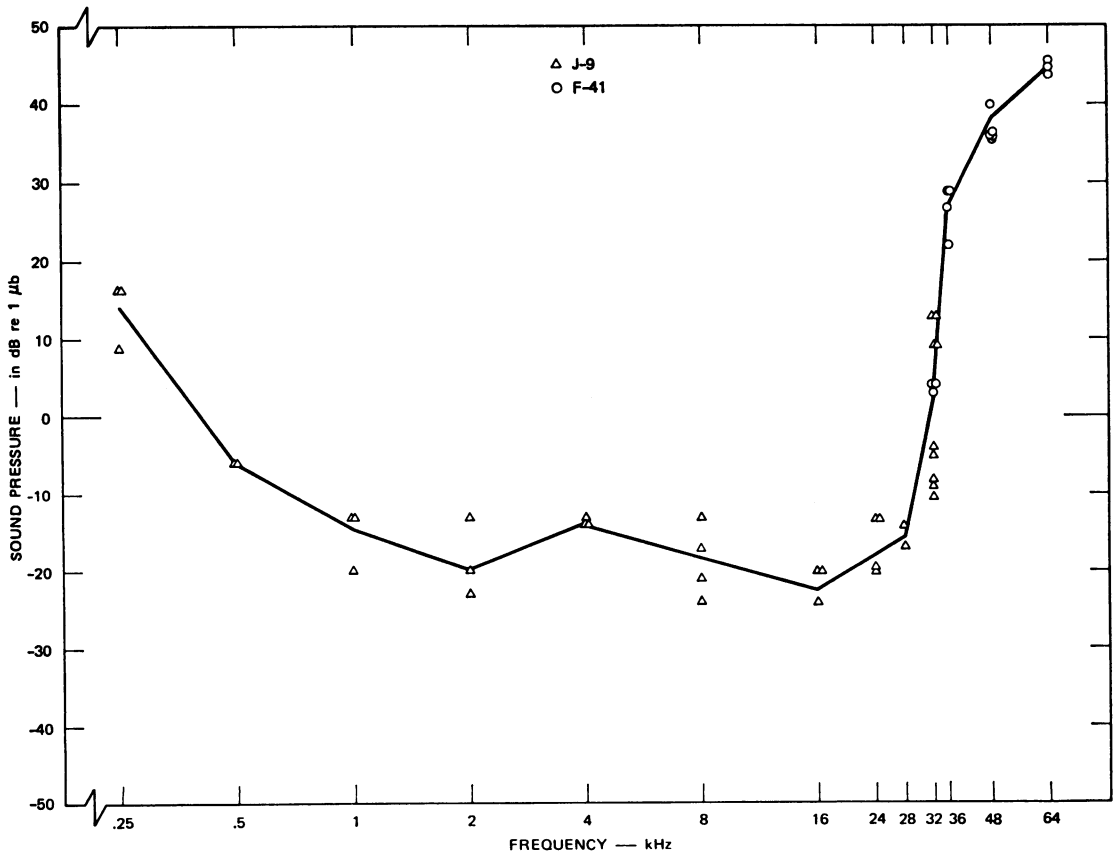


Fig. 4. Underwater audiogram for California sea lion (Sam).

density of the organ of Corti. For example, a high density of ganglion cells is broadly distributed in man and cat, both having a wide range of sensitivity (Schuknecht, 1960; Wever, 1949).

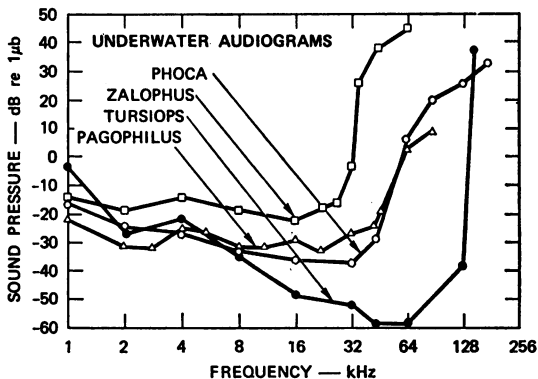


Fig. 5. Comparison of underwater audiograms of *Zalophus* (this study), *Phoca* (Mohl, 1968a), *Phogophilus* (Terhune and Ronald, in press) and *Tursiops truncatus* (Johnson, 1966).

#### Upper Frequency Limit

Between 28 and 36 kHz, the sea lion underwater audiogram has a very steep slope of about 60 dB/octave, and, between 45 and 64 kHz, the seal audiogram also has a very steep slope of about 60 dB/octave. These rates of loss in sensitivity at high frequencies are indicative of the existence of a conventional high frequency cutoff. However, the slope of the sea lion audiogram above 48 kHz decreases substantially to about 14 dB/octave, while the slope of the seal audiogram above 64 kHz also decreases substantially to about 12 dB/octave. This characteristic change in the slope of the audiogram from very steep to moderate at the higher frequencies closely resembles, as pointed out by Møhl (1968a), the ultrasonic bone conduction threshold in humans (Corso, 1963). Although human subjects can discriminate between the intensity of these ultrasonic frequencies, they are incapable of making a frequency discrimination (Corso and Levine,

1965). Paralleling the lack of frequency discrimination in humans of bone-conducted ultrasonics, Møhl (1967) found that, although the harbor seal has good frequency discrimination under water below 60 kHz, frequencies above this value are not differentiated. For this reason, Møhl (1967) logically classified such frequencies as ultrasonics despite their demonstrated audibility in the seal. In the case of the sea lion, the high frequency cutoff is probably between 36 to 48 kHz, and one would predict on the basis of Møhl's results that, in the sea lion, discrimination of frequencies above 48 kHz is either nonexistent or very poor, *i.e.*, the  $\Delta F$  would be rather large. Although the upper limit of underwater hearing in the California sea lion is at least one-half octave below that of the harbor seal, the similarity in the slope changes at the upper frequencies suggests that some seals (phocids) and some sea lions (otariids) use two distinct mechanisms for hearing under water. One is conventional and allows for frequency discrimination. The other, probably bone conduction, is used for ultrasonic detection requiring relatively intense sounds to be perceived and does not apparently allow for frequency analysis.

Additional support for the notion that the sea lion depends on a different mechanism for detecting sounds under water above the frequency of 36 kHz comes from some miniature experiments or preliminary observations that were conducted while obtaining the sea lion audiogram. Although the sea lion had some initial difficulty at 32 kHz, a smooth psychophysical function was nevertheless obtained. However, the next frequency tested (48 kHz) initially produced no response even when very intense signals were used. Eventually, after a good deal of exposure, the sea lion responded to intense tones of 48 kHz. On returning to 8 kHz, the sea lion at first did not respond, and additional training at this frequency was necessary. Two additional transitions to frequencies above and below 32 kHz yielded similar results. Thus, the sea lion repeatedly failed initially to transfer its lower frequency (1 to 32 kHz) experience to tones of higher frequency (48 to 64 kHz) and *vice versa*, despite the fact that transfer among the lower and the higher frequencies was always perfect. These observations suggest that the sea lion detected tones below 32 kHz as radically or qualitatively different from tones of 48 and 64 kHz. After

moving back and forth several times between sonic and ultrasonic frequencies, the sea lion learned to shift readily from one mode of detection to the other. Furthermore, after extensive training at 64 kHz, intense tones at frequencies of 96, 128, and 192 kHz did elicit vocalizations.

#### *Comparative Anatomy of the Pinniped Ear*

Although extensive work has been done on the anatomy of the cetacean ear, information currently available on the comparative anatomy of the pinniped ear is almost negligible. Møhl (1968b) did some preliminary anatomical work comparing some middle ear structures of the California sea lion with those of one adult harbor seal. Pinnipeds have oversized ossicles compared with other terrestrial mammals. The weight of the sea lion ossicles was 18 mg compared with 204 mg in the seal. An increase in weight of the auditory ossicula chain from otariids to phocids to sirenians is thought to reflect the degree to which these mammals are adapted to a marine life. Also Møhl found that the area of the tympanic membrane of the sea lion was about 30 mm<sup>2</sup> and that of the seal about 120 mm<sup>2</sup> and that the area of the tympanic membrane to that of the footplate of the stapes was 23:1 in the sea lion and 28:1 in the seal (Møhl, 1968b).

#### *Pinniped versus Porpoise Hearing*

Despite some important differences between the underwater hearing of an otariid (*Zalophus*) and a phocid (*Phoca*), there are enough similarities to justify a comparison of the audibility of pinnipeds with that of the porpoise on several parameters (see Figure 5).

The lowest thresholds of the porpoise (between 40 and 80 kHz) lie one to two octaves above those of the seal and sea lion. The sensitivity of the porpoise is greater than the sea lion or seal at frequencies above 4 kHz. In addition to this general superiority in sensitivity, the lowest threshold of the porpoise (−58 dB re 1  $\mu$ b at 50 kHz) is about 21 dB lower than the lowest threshold of the seal (−37 dB re 1  $\mu$ b at 32 kHz) and about 36 dB lower than the lowest threshold of the sea lion (−22 dB re 1  $\mu$ b at 16 kHz). The high-frequency cutoff in the porpoise is approximately 145 kHz with evidence of frequency

discrimination at this upper limit, while the high-frequency cutoff in the seal is 60 kHz and in the sea lion, about 36 kHz. There is strong evidence that the sensitivity of both forms of pinnipeds to higher frequencies is due to some form of "pseudo hearing", probably bone conduction, which is apparently unrelated to the frequency parameter. Thus, according to Møhl's definition of ultrasonics, there would appear to be "seal ultrasonics" and "sea lion ultrasonics", each beginning at different frequencies.

The above description of the comparative underwater hearing of marine mammals clearly demonstrates that some seals and sea lions are more similar to one another in this regard than they are to an odontocete cetacean, the Atlantic bottlenosed porpoise. The differences are great enough so as not to be attributed to methodological factors or errors of sampling and measurement. Underwater auditory sensitivity from 16 to 128 kHz in the three pinniped forms thus far investigated is far inferior to that of the porpoise, a marine mammal known to depend on echo-location for food-finding and navigation. It does not seem unreasonable to assume that echolocation was a major source of selective pressure for excellent hearing sensitivity at frequencies above 60 kHz, in the totally aquatic porpoise. The amphibious pinnipeds are generally not believed to depend on echolocation to the extent that some whales and porpoises do (Schusterman, 1966; Schusterman, 1967; Schusterman, 1968). Furthermore, the amphibious nature of their existence requires the pinnipeds to have relatively good hearing, both under water and in air [recently demonstrated in both the harbor seal (Møhl, 1968a) and the harp seal (Terhune and Ronald, 1971)], and such a requirement may have limited the development of high-frequency hearing under water. The fact that the pinniped's high-frequency cutoff under water is two octaves above that of apes and man in air does not vitiate this argument, since recent research suggests that the capability of hearing frequencies between 20 and 60 kHz without depending on bone conduction or some other method seems to be a general characteristic of mammals (with Anthropoid Primates being the exception rather than the rule) and not necessarily a specialized adaptation (Master-son, Heffner, and Ravizza, 1969).

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